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Stratigraphic distribution and suggested evolution of dendroid graptolites from the Silurian of eastern Australia

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Abstract

Five evolutionary lineages are proposed for Silurian species of the benthic dendroid graptolite genus Dictyonema, based largely on the exceptional eastern Australian records of the genus, comprising at least 25 species. These are: A, the delicatulum lineage with bifurcating ventral autothecal apertural spines; B, the paululum lineage with single ventral apertural spines or processes; C, the elegans lineage with isolated thecal apertures ± processes; D, the sherrardae lineage with dorsal apertural processes; and E, the venustum lineage with simple autothecal apertures. Brief comments are also made on other dendroid genera occurring in Australian strata, namely: Acanthograptus, Koremagraptus, Callograptus, Dendrograptus, Stelechocladia, Thallograptus and Palaeodictyota. Other non-graptoloid benthic hemichordates also listed are the tuboids Galaeograptus, Reticulograptus and Cyclograptus and the rhabdopleuran ?Rhabdopleura. Age ranges of all the species attributable to all of the above genera are tabulated.

Keywords

Silurian, Australian dendroids, graptolites, Dictyonema, lineages, GeoQUEST

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Stratigraphic distribution and suggested evolution of dendroid graptolites from the Silurian of eastern Australia

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Five evolutionary lineages are proposed for Silurian species of the benthic dendroid graptolite genus *Dictyonema*, based largely on the exceptional eastern Australian records of the genus, comprising at least 25 species. These are: A, the *delicatulum* lineage with bifurcating ventral autothecal apertural spines; B, the *paululum* lineage with single ventral apertural spines or processes; C, the *elegans* lineage with isolated thecal apertures ± processes; D, the *sherrardae* lineage with dorsal apertural processes; and E, the *venustum* lineage with simple autothecal apertures. Brief comments are also made on other dendroid genera occurring in Australian strata, namely: *Acanthograptus*, *Koremagraptus*, *Callograptus*, *Dendrograptus*, *Stelechocladia*, *Thallograptus* and *Palaeodictyota*. Other non-graptoloid benthic hemichordates also listed are the tuboids *Galaeograptus*, *Reticulograptus* and *Cyclograptus* and the rhabdopleuran ?*Rhabdopleura*. Age ranges of all the species attributable to all of the above genera are tabulated.

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Keywords: Silurian, Australian dendroids, graptolites, *Dictyonema*, lineages.

RESEARCH on Australian Silurian graptolites has revealed that benthic dendroid graptolites are much more common than previously supposed (e.g. Rickards *et al*. 2003), and that they exhibit considerable diversity, particularly in the case of *Dictyonema* J. Hall, 1851. Llandovery (early Silurian) strata in Australia have yielded probably the most diverse dendroid fauna yet known, especially in the upper part of the series.

At least 25 Silurian species of *Dictyonema* have been identified (Rickards *et al*. 1995, 2003, 2005, 2009; Rickards & Jell 2002; Rickards & Wright 1997, 1999, 2001), and their evolution is discussed below. All these records, apart from the Queensland graptolites documented by Rickards & Jell (2002), are from New South Wales; no Victorian dendroids were mentioned by Rickards & Sandford (1998) but some were described by Harris & Thomas (1948). No Australian Silurian dendroids are known outside Victoria, Queensland and New South Wales.

For general information and important reviews of Australian Silurian biostratigraphy the reader is directed to Pickett *et al*. (2001), Talent *et al*. (2003) and Strusz (2007).

Preservation of graptolites often poses problems, and dendroid graptolites can be particularly difficult because the rhabdosomal stipes are often narrow and the constituent thecae small and thread-like. Furthermore, many colonies are preserved with the thecae facing normal to bedding (either upwards or downwards), and hence the stipe may be seen in dorsoventral view obscuring the autothecal profile as well as the apertural processes. As a result, dendroids are often described in general terms based on the overall shape and colony dimensions: whether it is conical or flabellate; small or large; or has a holdfast or 'roots'. The shape of the colony, whether conical, flabellate or of some other form, is itself often difficult to determine and there is no certain information as to whether or not rhabdosomal form is a species-specific character. Many species of *Dictyonema* have quite similar combinations of these attributes and to distinguish them – to identify them – it is necessary to measure more closely stipe and dissepimental dimensions and, if possible, to identify the nature of the autothecae.

In this paper we rely heavily on the nature of the autothecae, coupled with other biocharacters such as stipe spacing; lateral and dorsoventral stipe width; nature, size and frequency of dissepiments; nature of interstipe spaces; branching patterns;

A *delicatulum* lineage: species with bifurcating ventral, apertural processes or spines
D. delicatulum delicatulum Lapworth, 1881: late Llandovery
D. elongatum elongatum Bouček, 1957: Přídolí
D. e. subelongatum Rickards *et al*., 1995: ?Llandovery to Ludlow
D. delicatulum sp. cf. *D.delicatulum* Lapworth, 1881: late Llandovery
D. regulare Bouček, 1957 (+ *D*. sp. of Rickards *et al*., 1995) *nilssoni* Zone (Ludlow)
D. d. barnbyensis Rickards & Wright, 1997: late Ludlow (cf. is Přídolí)
D. sp. A, Rickards & Wright, 1997: late Ludlow
D. sp. 1, Rickards *et al*., 2003: early *griestoniensis* Zone (Llandovery)
D. sp., Rickards *et al*., 1995: *nilssoni* Zone (Ludlow)
B *paululum* lineage: species with single ventral, apertural spatula-like spine or process
D. paululum paululum Bulman, 1928: *turriculatus* Zone (Llandovery)
D. p. *hanoverense* Rickards *et al*., 2003: *parultimis* Zone (Přídolí)
D. p. australis Rickards & Jell, 2002: early *crenulata* Zone to *griestoniensis* Zone (Llandovery)
D. zalasiewiczi Rickards *et al*., 2009: *turriculatus* Zone (Llandovery)
C *elegans* lineage: species with both ventral and dorsal apertural margins isolated.
D. elegans Bulman, 1928: late Wenlock to Ludlow.
D. williamsae Rickards *et al*., 2003: early *griestoniensis* Zone (Llandovery)
D. warrisi Rickards *et al*., 2003: early *griestoniensis* Zone (Llandovery)
D *sherrardae* lineage: species with pronounced dorsal apertural processes
D. sherrardae sherrardae Rickards *et al*., 1995: *nilssoni* Zone to late Ludlow
D. s. *mumbilensis* Rickards & Wright, 1997; late Ludlow
D. jenkinsi Rickards *et al*., 2003: early *griestoniensis* Zone (Llandovery)
D. sp. nov.: *riccartonensis* Zone*
E *venustum* lineage: species with simple autothecal apertures or short denticles.
D. venustum Lapworth, 1881: *turriculatus* to *griestoniensis* Zones
D. g. krafti Rickards & Wright, 1997: late Ludlow
D. favosum Sherrard, 1956: *nilssoni* Zone (Ludlow)
D. subtile Bouček, 1957: Ludlow
D. cf. *subtile* Bouček, 1957: *nilssoni* Zone (Ludlow)
D. falciferum Bulman, 1928: *crispus* to *griestoniensis* Zones (Llandovery)
D. muirae Rickards *et al*., 2003: *turriculatus* to *griestoniensis* Zones (Llandovery)
D. sp. cf. *D. corrugatellum* Lapworth, 1881: *turriculatus* to upper *riccartonensis* Zone*

Table 1. List of Australian *Dictyonema* species in autothecal groupings and with age attributions, based on Australian and non-Australian material.

and (occasionally) bithecal type. In Table 1 we list the species of *Dictyonema* relevant to the lineages we describe below, together with a summary of the autothecal type; the known age of each species (usually dated with graptoloids); and authorship. Table 2 gives the measurements, so far as possible, for all the Australian dictyonemid species, together with a sketch of the thecal type and apertural apparatuses. We have cited unpublished research (Rickards *et al*. in prep.) on species of dendroids from both the Quarry Creek and Four Mile Creek areas near Orange, New South Wales and, where necessary, draw particular attention to these taxa in the figures and text.

THECAL TYPES

A summary of Bulman's (1928, 1933) autothecal and bithecal types was given by Rickards *et al*. (2003, fig. 4) and this is reproduced here as Figure 1. The present work modifies this scenario in that: (a) Figure 1J depicts a single ventral spine whereas we now know that long, bifurcating spines occur in Silurian dictyonemids; and (b) Figure 1L shows a single dorsal process, whereas

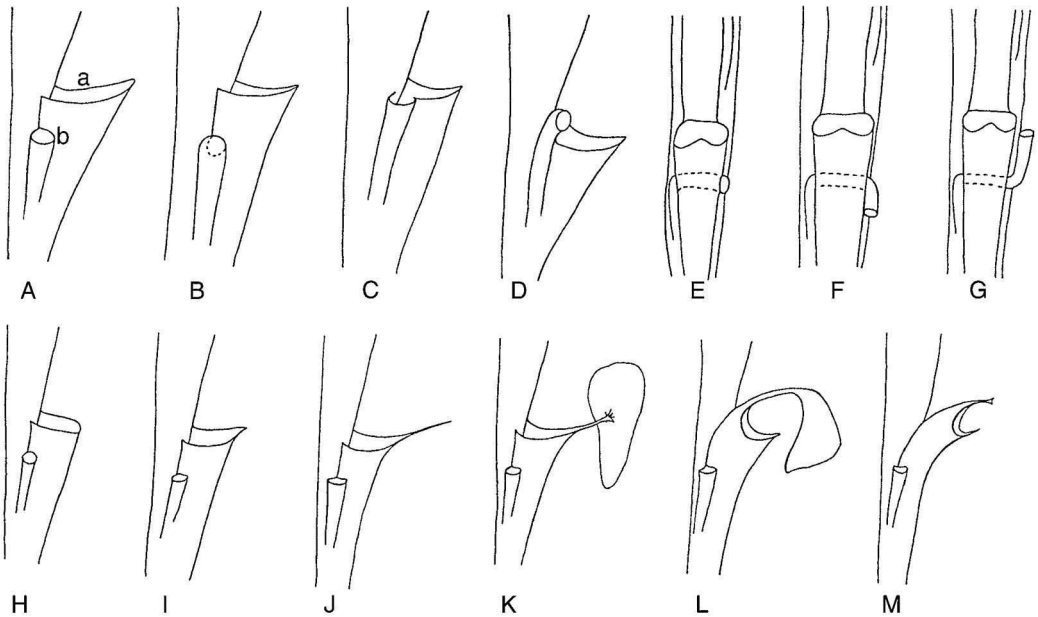


Figure 1. Autothecal and bithecal types in Silurian *Dictyonema* species. **A-G**, different types of bithecae. **A**, Bulman's (1928, 1933) Type 1 with bitheca n+1 opening along the lateral wall of autotheca n.This is the most common of autothecal/bithecal relationships. **B-C**, Bulman's (1928, 1933) Type 2 in which the bithecal aperture opens inside the autothecal tube or aperture. **D**, Bulman's (1928, 1933) Type 3 where the n+1 bithecal aperture is located on the dorsal side of the aperture of autotheca n. **E**, Bulman's (1928, 1933) Type 4 in which the bithecal tube n+1 passes between the dorsal wall of autotheca n and the ventral wall of autotheca n+ 1. **F-G**, Bulman's (1928, 1933) Type 5 a modification of Type 4 in which the bithecal tube turns proximally or distally before the bithecal aperture is reached. **H–M**, autothecal variation in *Dictyonema* species. **H**, autothecal aperture is the termination of a simple tube. **I**, the ventral lip projects as a short, sharp denticle; **J**, the ventral lip projects as a spine which may or may not bifurcate. **K**, the ventral process is adorned with a large shield-like plate. **L**, the dorsal apertural process has plate-like process hanging more or less in front of the aperture. **M**, the apertural region is isolated from the ventral wall of the next autotheca; for the sake of simplicity in H–M the Type 1 bithecal arrangement is shown; fuselli omitted. a, autothecal aperture; b, bithecal aperture; these structures are described or commented upon in various places in the text. Based on Australian and non-Australian material. Reproduced with permission of the Australian Museum from Rickards et al. (2004).

we now have a specimen in which this process bifurcates or, possibly, is bispinose.

Autothecal types

It is concluded that, whereas dimensions and autothecal spacings may change from species to species, autothecal type is consistent within the lineages we propose below:

A. The *delicatulum* lineage (early *griestoniensis* Biozone [Llandovery] to Přídolí), characterised by autothecal apertures possessing long, pronounced, bifurcating ventral spines.

B. The *paululum* lineage (late Llandovery to *parultimus* Biozone [Přídolí]), characterised by a single ventral autothecal spine or shorter denticle.

C. The *elegans* lineage (early *griestoniensis* Biozone [Llandovery], to Ludlow), characterised by both ventral and dorsal apertural margins being isolate.

D. The *sherrardae* lineage (early *griestoniensis* Biozone, Llandovery, to *inexspectatus* / *kozlowskii* biozones, late Ludlow) with pronounced dorsal apertural processes.

E. The *venustum* lineage (*crispus* Biozone, Llandovery, to Emsian, late Early Devonian), with more or less simple apertures, possibly with a slight denticle in some.

Bithecal types

It is not easy to relate these five lineages to Bulman's (1928) bithecal types, primarily because of a lack of information. Thus, in the *delicatulum* lineage, consisting of 7 or 8 species, almost nothing is known about the bithecal type. Bulman (1928) thought that *D. delicatulum* might have had internally opening bithecae (his group 2, see Fig. 1B).

In the *paululum* lineage, bithecae of only *D. p. paululum* and *D. p. australis* are known. The former subspecies has diminutive, simple, external bithecae, and the latter possibly has Bulman's

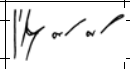
Species	Autothecal Type	Autothecal Spacing	Stipe Spacing	Dissepiment Spacing (per 10 mm)	Dissepiment Type	Dorsoventral Width (mm)
LINEAGE A						
D. d. delicatulum Lapworth, 1881		22-24	22-23	10 to 12	fine	0.3-0.5 mm
D. e. subelongatum Rickards *et al.,* 1995		20-25	10 to 18	3 to 5	fine	0.5-0.7 mm
D. d. barnbyensis Rickards & Wright, 1997		20-24	10 to 30+	10 to 30	fine	0.6-0.8 mm
D. sp. cf. *D. d. delicatulum* Rickards *et al.,* 2003		20-25	20	14-18	fine to robust, up to 0.1	?0.5 mm
D. sp. A of Rickards & Wright 1997		?20		?10		
(?= *D. d. barnbyensis*)						
D. sp. of Rickards *et al.*, 1995		30			robust	0.6 mm plus spine
LINEAGE B						
D. p. paululum Bulman, 1928		19-20	20	< 20	0.03	0.4-0.6 mm
D. paululum hanoverense Rickards *et al.*, 2005		28-30	16	?30	fine	0.5 mm
D. p. australis Rickards *et al.,* 2003		20-30	16-20	12-20, closer distally	fine	0.3-0.5 mm
D. zalasiewiczi Rickards *et al*., 2009		*ca* 20	0.2-0.3	30-40	?	?0.05-0.1 mm
LINEAGE C						
D. elegans Bulman, 1928		22-30	>30	14-16	robust, 0.05	0.4-0.5 mm
D. williamsae Rickards *et al.,* 2003		13	8 to 12	6 to 7	0.15-0.2, arched	0.6-0.7 mm
D. regulare Boucek, 1957 (see Rickards *et al*. 1995)		20-30	11 to 15	4 to 10	fine or robust	1.5 mm including spines
D. warrisi Rickards et al., 2003		28		12 (variable)		0.2-0.35 mm +1.0 mm spines
LINEAGE D						
D. s. sherrardae Rickards *et al.,* 1995		15-25	10 to 15	26-18	some phrygian	0.7-0.8 mm, rarely 1.2 mm
D. jenkinsi Rickards *et al.*, 2003		16	14	18-20	hair-like	0.8 mm (1.3 mm with processes)
D. s. mumbilensis Rickards & Wright, 1997		25-30		13-14	robust, some phrygian	0.5-0.7 mm
D. sp. nov.						
LINEAGE E						
D. venustum Lapworth, 1881		14-30	10 to 18	5 to 8	0.1-0.25	0.4-0.6 mm, some thick
D. falciferum Bulman, 1928		20	12 to 19	5 to 12	fine	0.4-0.6 mm
D. g. krafti Rickards & Wright, 1997		20-25	13-16	3 to 7	robust	0.5 mm
D. muirae Rickards *et al.,* 2003		40	14-20	few	?	0.6 mm
D. favosum Sherrard, 1956		30	13-18	5 to 10	fine, or robust	
D. sp. cf. *D. subtile* Bouček, 1936		20	11 to 13	15	fine	0.4 mm
D. corugatellum Lapworth, 1881	?simple	18-20	17-18	10 to 20	fine	?0.3 mm

Table 2 (above and opposite). Australian *Dictyonema* species with all known biocharacter features and measurements tabulated; species are arranged in autothecal groupings; based on Australian and non-Australian material.

Bithecal Type	Branching intervals	Interstipe Spaces (mm)	Rhabdosome Form	Rhabdosome Size	Stem/Holdfast	Lateral Stipe Width (mm)	Age
inconspicuous, ?internally opening	irregular	0.3-0.4	cyathiform, short thick	50 mm+	"roots"	0.2-0.3	late Llandovery
	irregular, infrequent	0.4-0.7	?flabellate	30 mm+		0.1-0.3	late Llandovery
	irregular	0.3-0.4	conical	35 mm+	basal disc 2 mm	0.15-0.2	late Ludlow
?	irregular	0.15-0.5	conical		basal disc 1-2 mm	0.2-0.3	*griestoniensis* Zone
?	3 branching zones	0.1-0.5	conical		basal disc 1-2 mm	0.25-0.3	late Ludlow
	proximally 1-2 mm						
?Bulman type 5, robust						0.3	*nilssoni* Zone
Bulman type 1	irregular	0.5-0.6	conical	20 mm		0.15-0.2	*turriculatus* Zone
							parultimus Zone
	zoned 1.5-2.0, latter distally		conical	30 mm		0.1-0.2	*griestoniensis* to *crenulata* Zones
	in zones	0.5	fan-shaped	30 mm long		0.2-0.3	late Llandovery
?Bulman type 1		0.4-0.6	conical	20 mm +		0.2-0.3	
	branching irregular		conical	14 mm	disc 2 mm	0.15-0.3	*griestoniensis* Zone
Bulman type 5	very roughly 2 mm at 1-2 mm	0.5-1.0	?flabellate	50 x 78 mm	holdfast	0.2-0.75	*nilssoni* Zone
in autothecal angle, Bulman type 4	zoned, ?5 mm distally	0.4-0.6	conical			0.3-0.4	*griestoniensis* Zone
	irregular, 1-2 mm		conical	30 mm	stem, basal disc	0.3-0.5	*nilssoni* Zone (?late Wenlock)
Bulman type 5	zoned 2-3 mm less proximally		?conical	25 mm	holdfast	0.3-0.5	*griestoniensis* Zone
						0.2-0.3	late Ludlow
			?conical or flabellate			0.2-0.25	*riccartonensis* Zone
?Bulman type 3	irregular	0.5-0.9	?conical	35 mm	basal disc	0.2-0.4	*turriculatus* & *griestoniensis* Zones
?Bulman type 3-5	1 mm proximally, 2 mm distally	0.3-0.5	?conical	50 mm		0.2-0.3	*crispus* & *griestoniensis* Zones
tiny, in autothecal angle	irregular, 1-3 times each stipe	0.3-0.7	?conical	35 mm+	basal disc	0.2-0.25	late Ludlow
isolated, curved, modified Bulman type 5	1 mm proximally, wider distally	1	conical		holdfast	0.3-0.4	*griestoniensis* Zone
	10 mm	0.5-0.8	conical			0.25	Ludlow
	0.1 mm proximally	0.5-0.8	?flabellate		stem, basal disc	0.1-0.17	
		0.2-0.4				0.3	upper *riccartonensis* Zone

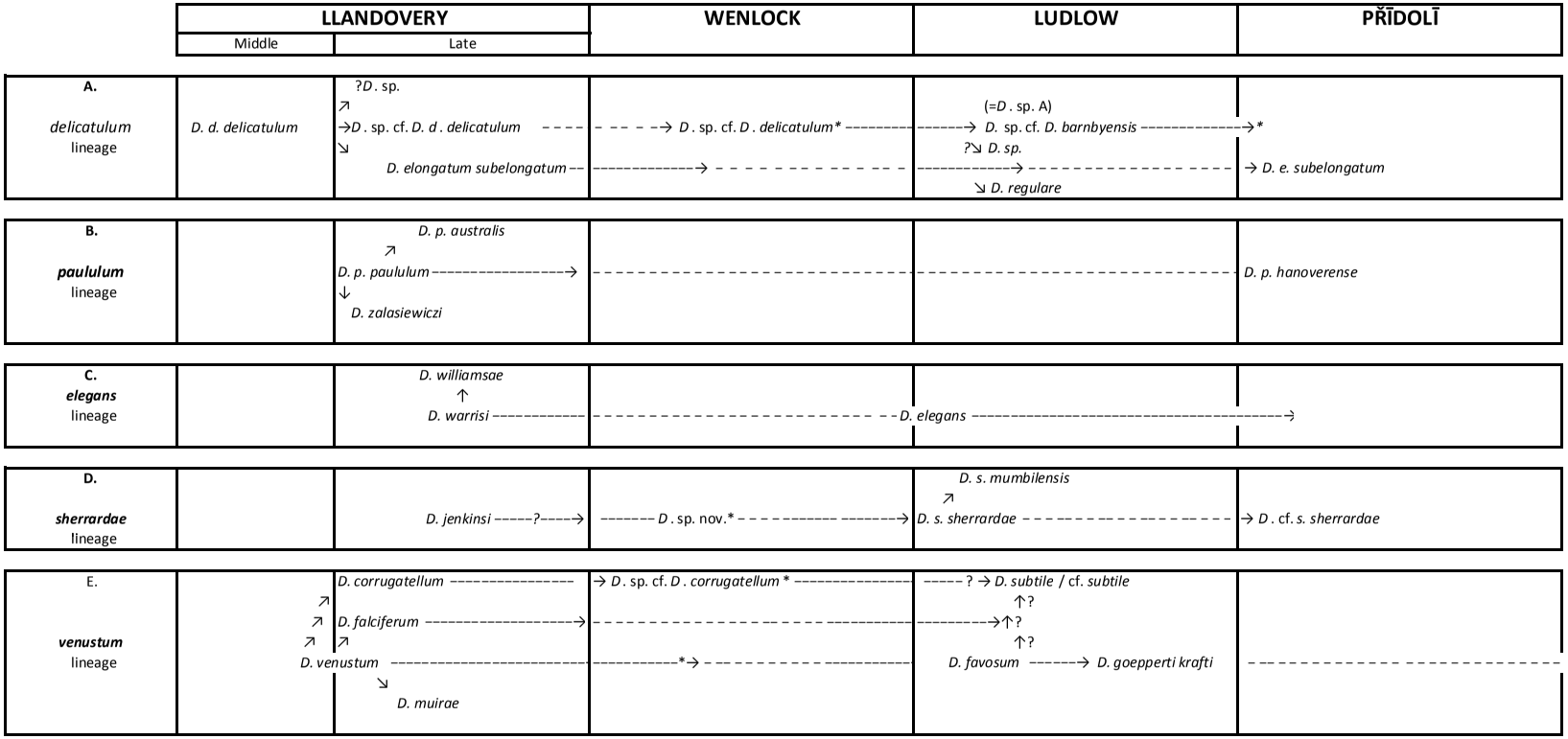


Figure 2. Diagram showing evolutionary *Dictyonema* lineages proposed in this paper; * indicates unpublished results from ongoing studies.

(1928) type 4 or 5 bithecae (Fig. 1E-G).

The *elegans* lineage exhibits considerable variation in bithecal nature: *D. warrisi* has type 3 (Fig. 1D), whereas *D. regulare* and possibly *D. elegans* have type 5 (Fig. 1G).

Only the *sherrardae* lineage is consistent in terms of bithecal type; both *D. sherrardae* and *D. jenkinsi* have type 3 bithecae, with the bithecal aperture openings between the autothecal apertural margin and the ventral wall of the succeeding autotheca. The remaining lineage, *venustum*, has either type 3 or type 5 bithecae, but the bithecal type is unknown in most species of this lineage.

One other major problem concerns the use of bithecae in classification; as change may occur along the rhabdosome, several of Bulman's types can be found on the one colony (e.g., *D. falciferum*). In this respect the bithecae can be contrasted with autothecae which are almost uniform in size and nature, certainly in Silurian species.

DISSEPIMENTS

Bouček (1957) divided Silurian dictyonemids into two groups, those with slender dissepiments and those with robust ones. This yields only a limited basis for subdivision of the group, although it is true that the *elongatum* and *paululum* lineages have mostly fine dissepiments, while those of the *sherrardae* lineage are robust. However, the *elegans* and *venustum* lineages have a mixture, with some species (e.g., *D. elegans*, *D. warrisi* and *D. sherrardae*) exhibiting both. Furthermore, the dissepiments thicken in old age in a colony as more strengthening cortical tissue is added. Dissepimental type is not, therefore, a useful classificatory tool in the light of currently available information.

VALUE OF DENDROIDS IN SILURIAN STRATIGRAPHY

Although it is very likely that dendroids will never provide the stratigraphic precision of the planktonic graptoloids, our work has shown that the following faunas are easy to identify: mid-late Llandovery; late early Wenlock; late Wenlock; early Ludlow; late Ludlow; and Přídolí. It is perhaps surprising that benthic graptolite species could have had such wide palaeogeographic distribution; there is, nevertheless, often a strong endemic component in the overall assemblage as noted by Rickards *et al*. (2003).

In some sequences, particularly those deposited in shallower or inshore sequences, benthic dendroid graptolites may outnumber graptoloids: indeed, the latter may even be absent. In such circumstances, the recovered dendroids may resolve the age of the rock, down to one or two stages if not (graptoloid) biozones. Figure 3 is a range chart of the Australian Silurian dendroids (exclusive of *Dictyonema*), and some tuboids, so far identified. The main papers forming the basis of this paper and dealing with dendroid faunas, and the relevant localities, are: Sherrard (1954, 1956, 1962: Yass, NSW); Harris & Thomas (1948, Eildon Dam, Victoria); Rickards *et al*. (1995, Quarry Creek, NSW); Rickards & Wright (1997, Newrea, NSW); Rickards & Wright (1999, Yass, NSW); Rickards & Wright (2001, Limekilns, NSW); Rickards & Jell (2002, North Queensland); Sherwin & Rickards (2002, Cheesemans Creek, NSW); Rickards *et al*. (2004, Four Mile Creek, NSW); Rickards *et al*. (2005, Wellington area, NSW) and Rickards *et al*. (2009, Cotton Hill, NSW).

In Figure 3 we illustrate several other features. Although there is a clear monographic component, there is a lack of dendroids in the oldest and middle Wenlock: this interval may be represented by the Quarry Creek Limestone (yielding no graptolites) near Orange, New South Wales and the Quarry Creek Hiatus (see Rickards *et al*. 2003 for summary). The lack of dendroids (and rarity of graptoloids) in the middle Ludlow (roughly *scanicus* to *aversus* biozones) may be a collecting failure, may reflect unrecognised hiatuses, or may reflect sea level lowstands.

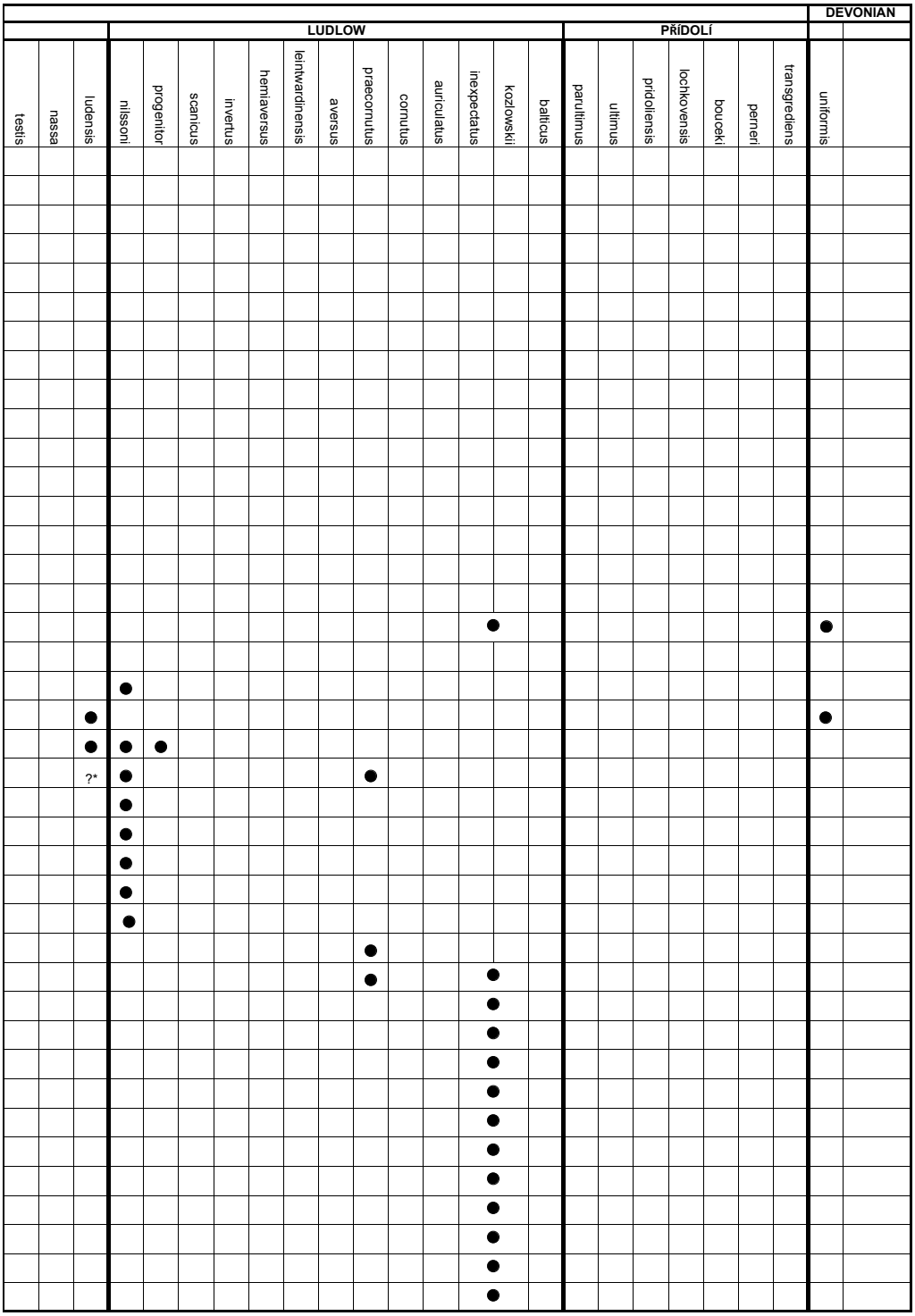
Lastly, Figure 3 illustrates the absence, to date, of any dendroids other than *Dictyonema* from the Přídolí. It does seem peculiar that, with some 15 dendroid genera known from the Llandovery to Ludlow, only one genus occurs in the Devonian (a single poorly preserved specimen of *Dendrograptus* was recorded by Rickards & Wright [2001] from the Early Devonian). This absence of Přídolí dendroids cannot be an extinction event, but must reflect environments with which *Dictyonema* species were able to cope, albeit in reduced circumstances, although other genera were not. Many Silurian dendroid genera and species prior to the Přídolí have robust rhabdosomes with thick stipes and often exhibit stipe anastomosis. It is conceivable that they are adapted for more turbulent environments than *Dictyonema* and ?*Dendrograptus*. Nevertheless, *Dictyonema* species also thrived at this time, comprising almost half the recorded number of species; and, as we point out in the section of evolution, the slight tendency in some of lineages to develop hydrodynamically stronger colonies up sequence is puzzling.

EVOLUTION OF THE *DELICATULUM* LINEAGE

The *delicatulum* lineage includes forms which

Species	SILURIAN													
	LLANDOVERY							WENLOCK						
	gregarius	convolutus	sedgwickii	turriculatus	crispus	grestoniensis	crenulata	centrifugus	murchisoni	riccartonensis	rigidus	flexilis	ellesae	testis
Stelechocladia praeattenuata Rickards *et al.,* 2003	aff.			cf.		●				cf.				
Callograptus bridgecreekensis Rickards *et al.,* 2003				●		●								
Callograptus rigbyae Rickards *et al.,* 2003				●		●				cf.*				
Callograptus ulahensis Rickards *et al.,* 2003				aff.	●					●*				
Acanthograptus p. praedeckeri Rickards *et al.,* 2003				●		●								
?Rhabdopleura sp. Rickards & Wright, 2009 R				●										
Acanthograptus p. minimus Rickards *et al.,* 2003					●									
Dendrograptus avonleaensis Rickards *et al.,* 2003						●								
Dendrograptus ashburniaensis Rickards *et al.,* 2003						●								
Callograptus sp. cf. *D. niagarensis* Spencer, 1878						●								
Pseudodictyonema graptolithorum (Počta, 1894)						●								
Thallograptus christoffersonae Rickards *et al.,* 2003						●●								
Koremagraptus elegantulus Rickards *et al.,* 2003						●								
Koremagraptus obscurus Rickards *et al.,* 2003						●								
Reticulograptus thomasi Rickards *et al.,* 2003 T						●								
Cyclograptus? australis Rickards *et al.,* 2003 T						●								
Dendrograptus sp. cf. *D. praegracilis* Spencer, 1884 *										●				
Dendrograptus sp. cf. *D. parallelus* Shrock, 1928 *										●				
Galeograptus? sp.										●*				
Dendrograptus sp.														
Ptilograptus d. discurrens Sherrard, 1956														
Acanthograptus a. aculeatus (Počta, 1894)														
?Dendrograptus sp.														
Palaeodictyota sp. aff. *D. undulatum* (Počta, 1894)														
Thallograptus nullus (Pocta, 1894)(=,pars, *Cactograptus* Harris & Thomas, 1948)														
Thallograptus delicatus (Bouček,1957)														
Acanthograptus deckeri Bouček,1957 *														
Dendrograptus typhlos Rickards *et al.,* 2005														
Thallograptus acanthicus vandenbergi Rickards & Wright, 1997														
Callograptus ?pulchellus Shrock, 1928, subsp. 1, Rickards & Wright, 1997														
Callograptus ?pulchellus Shrock, 1928, subsp. 2, Rickards & Wright, 1997														
Desmograptus quebecensis Ruedemann, 1947														
Stelechocladia talenti Rickards & Wright, 1997														
Stelechocladia struszi Rickards & Wright, 1997														
Acanthograptus a. neureaensis Rickards & Wright, 1997														
Palaeodictyota sp. cf. *P. flabellata* Ruedemann, 1947														
Thallograptus cooperi Rickards & Wright, 1997														
Koremagraptus plexus (Počta, 1894)														
Koremagraptus kalfusi praekalfusi Rickards & Wright, 1997														
Ptilograptus d. sherrardae Rickards & Wright, 1997														

Figure 3 (above and opposite). Range chart of Australian dendroid and tuboid graptolites, and one hemichordate (excluding *Dictyonema*, for which see Figs 1-2, Table 1). * indicates unpublished results from ongoing studies. R = rhabdopleuran hemichordate; T = tuboid graptolites.


DEVONIAN
LUDLOW
PŘÍDOLÍ
testis
nassa
ludensis
nilssoni
progenitor
scanicus
invertus
hemiaversus
leintwardinensis
aversus
praecornutus
cornutus
auriculatus
inexpectatus
kozlowskii
balticus
parultimus
ultimus
pridolensis
lochkovensis
boucekí
perneri
transgrediens
uniformis
?*

have bifurcating ventral appertural processes. In Figure 2 we depict suggested relationships within this group. *Dictyonema delicatulum delicatulum* may be a geographical subspecies related to the Australian form *D*. sp. cf. *D. d. delicatulum*, although Bulman's (1928) description, revising Lapworth's (1881) one, suggests that the Scottish forms may occur stratigraphically lower, in the *sedgwickii* Biozone. The Australian forms, from low in the *griestoniensis* Biozone, differ from Lapworth's types only in having slightly more densely spaced dissepiments (14-18 per cm compared with 10-12 per cm). *Dictyonema d. barnbyensis* from the late Ludlow (?=*D*. sp. A of Rickards & Wright 1997, also from the late Ludlow: see Table 2) differs from the eponymous subspecies in having more closely spaced dissepiments (10-30 per cm) and in having a small basal disc instead of a short thickened stem. We have no record of the species in the Wenlock but, if a straight line lineage is correct from *D. d. delicatulum* to *D*. sp. cf. *D. d. delicatulum* to *D. d. barnbyensis*, the morphological changes are relatively small, being an increase in dissepimental frequency and a flattening of the stalk to a basal disc. Both features would increase the ability of the colony to survive a more turbulent environment, and may reflect an adaption to the same.

In the Silurian, dictyonemids with bifurcating ventral spines occur in the Wenlock (*testis* Biozone; see Rickards *et al*. 1995, p. 22) and in the early Ludlow (*nilssoni* Biozone), but general rhabdosome and thecal details are lacking in available specimens: in one of these forms (Rickards *et al*. 1995, fig. 14F) the dissepimental style and spacing (12-16 per cm) is consistent with being an early Ludlow member of the lineage.

Dictyonema sp. 1 of Rickards *et al*. (2003, p. 318) from the *griestoniensis* Biozone also seems to have bifurcating thecal spines, although their origin is uncertain and the species is represented only by a single fragment with a low dissepimental spacing (8 per cm). We have tentatively included *D*. sp. 1 in this group but more material is needed to confirm relationships.

Dictyonema elongatum elongatum has been recorded from the Přídolí and Devonian of Bohemia (Bouček 1957) but not from Australia where, so far, we have identified *Dictyonema e. subelongatum* from the Ludlow. However, Bouček (1957, pp. 59-60, 170) recorded *D*. sp. aff. *D. elongatum* from the late Llandovery and the Wenlock. *Dictyonema elongatum* can, therefore, be regarded as a particularly long-ranging species; it is clearly related to *D. delicatulum*, having the same autothecal type, size and spacing, similar stipe spacing, stipe branching patterns and stipe dimensions. The main difference between the two species is the very low dissepimental spacings in *elongatum* (3-7 per cm) compared with *delicatulum* (10-30 per cm). We suggest that *Dictyonema e. subelongatum* separated from *D. delicatulum* at some point in the *sedgwickii-griestoniensis* level.

These closely related lineages exhibit some general evolutionary trends. Whereas the rhabdosome retains its overall proportions and size, there is an increase in the orderliness of the branching of the stipes, with more irregular branching in earlier forms. There is a small increase in dissepimental frequency in the *Dictyonema elongatum* line, but a greater increase in the same feature in the *Dictyonema elegantulum* line.

The overall colony form of the species in these two related lineages is uncertain. The colonies are large, probably mostly flabellate, but conical as in the case of *Dictyonema d. barnbyensis* (Rickards & Wright 1997, fig. 4C).

EVOLUTION OF THE *PAULULUM* LINEAGE

The *paululum* lineage comprises forms with a single autothecal ventral spine or process on the ventral aperture. In Figure 2 we show our suggested relationship of the taxa having this characteristic. *Dictyonema paululum paululum*, *D. p. australis*, *D*. sp. aff. *D. p. australis* and *D. zalasiewiczi* all appear in the *turriculatus* Biozone, but only the last is restricted to that level, the remainder ranging at least as high as the *griestoniensis* Biozone (late Llandovery). No representative of the *paululum* lineage has been found in the Wenlock or Ludlow, but one well preserved fragment of *Dictyonema p. hanoverense* is known from the *parultimus* Biozone (Přídolí).

The general similarity of *Dictyonema p. paululum* and *D. zalasiewiczi* can be seen from the illustrations of Rickards *et al*. (2009, figs 2a-b, 3c, 4a). In addition to the similar autothecal form, species in this group have similar dimensions for lateral and dorsoventral width, stipe spacing, autothecal spacing and the arrangement and branching patterns. All species in the group have quite high dissepimental spacing, much more than most dictyonemids, ranging from 12 per cm in places to 40 per cm, but the usual figure is closer to 20 per cm. *Dictyonema zalasiewiczi* has the highest dissepimental spacing we have recorded, of 30-40 per cm. We suggest a divergence of these forms in the late Llandovery involving primarily rapid increase in the number of dissepiments.

Dictyonema p. hanoverense, known from one well preserved fragment, shares the very high

dissepimental spacing and the other characters of the group, despite the considerable time gap between its occurrence in the Přídolí and the Llandovery forms; no species of this lineage has been found in the Wenlock or Ludlow.

The rhabdosomal form of this group is probably fan-shaped, and the only general evolutionary change seems to be a striking increase in the number of dissepiments. In this last change it resembles the *delicatulum* lineage discussed above.

EVOLUTION OF THE *ELEGANS* LINEAGE

The *elegans* lineage comprises forms with dorsoventral isolation and processes on the autothecal aperture. These forms have small to moderately sized, probably conical rhabdosomes and slender initial stipes (as seen both laterally and dorsoventrally in *D. warrisi* and *D. elegans*), and have high thecal spacing and moderate dissepimental spacing. Bithecae are of Bulman's (1928) groups 3-5 (i.e. rather "advanced"). The stratigraphically higher species, *D. williamsae* (Wenlock) and *D. regulare* (*nilssoni* Biozone, Ludlow), have similar general dimensions, but the dissepimental spacing decreases (6-7 per cm in *D. williamsae*, 3-5 per cm in *D. regulare*) as the stipes become a little more robust and the dorsoventral width increases. Later forms of *D. elegans* also have slightly more robust stipes. Accompanying the increase in robustness of the stipes are decreases in the autothecal spacing and stipe spacing.

The changes recorded for this lineage suggest a slight increase in the robustness of the rhabdosome, a trend noted above in the *delicalutum* lineage (but not in the *paululum* lineage), possibly related to a more turbulent environment. In the *paululum* lineage the number of dissepiments increases, as does the number and branching of the stipes; this lineage may also be universally adapting to rougher conditions.

EVOLUTION OF THE *SHERRARDAE* LINEAGE

The *sherrardae* lineage comprises forms with pronounced dorsal apertural processes. As suggested in Figure 2, *D. jenkinsi* may not be directly related to the rest of the *sherrardae* lineage. There is a considerable time gap (much of the Wenlock) where species of this group have not been found. However, *jenkinsi* and *sherrardae* both possess pronounced plates terminating the dorsal apertural spine. *Dictyonema* sp. nov. (under study by us) from the *riccartonensis* Biozone at Quarry Creek (Orange district, New South Wales) may be an intermediate between the two species. The main change from *jenkinsi* to *sherrardae sherrardae* is the development of phrygian dissepiments, a feature retained, though less common in the later *D. s. mumbilensis*. Not enough is known about *D*. sp. cf. *D. s. sherrardae* from the Přídolí, but it and *D. s. mumbilensis* have a more delicate appearance than either *D. s. sherrardae* or *D. jenkinsi*. Both may occur in generally quiet or lagoonal conditions, the former from the Booroo Ponds Group at Yass (Rickards & Wright 1999) and the latter from the Barnby Hills Shale near Wellington (Rickards & Wright 1997).

EVOLUTION OF THE *VENUSTUM* LINEAGE

The *venustum* lineage comprises forms with simple thecal apertures close to the parent stipe. It is likely that all these species had conical colonies and they are united in having quite high thecal spacings (up to 40 per cm in *D. muirae*) and rather low dissepimental spacings (mostly in the range of 3-8 per cm although *D*. sp. cf. *D. subtile* is an exception with 16 per cm).

The earliest member of the group is *D. venustum*, first appearing in the *turriculatus* Biozone and ranging into the *griestoniensis* Biozone. *Dictyonema falciferum* appears in the *crispus* Biozone and in the earliest *griestoniensis* Biozone along with *D. muirae*. The three species are clearly closely related, especially *venustum* and *falciferum* which differ primarily in thecal spacing and the fact that in *falciferum* the type 3-5 bithecae are a little more proximally curved at their extremities and have a clearer bithecal aperture (see Bulman 1928, p. 54-55). *Dictyonema muirae*, the last of the three to appear, is a little more advanced in its bithecae which, whilst of type 3-5, are also curved and free distally; the autothecal spacing is very high at up to 40 per cm.

As in the case of the previous lineage there is an absence of data in the Wenlock and the next records are of *D. favosum* and *D*. sp. cf. *D. subtile* in the *nilssoni* Biozone of the Ludlow. *Dictyonema favosum* is very similar to the late Llandovery forms, and also has a high autothecal spacing of 30 per cm. It also closely resembles the late Ludlow (*inexspectatus*/*kozlowskii* Biozone) *D. goepperti krafti* which Rickards & Wright (1997) considered a forerunner of the type subspecies from the Devonian of Bohemia. It seems likely that there is a simple lineage from *D. favosum* to *D. goepperti*, and that this probably arose from the Llandovery *D. venustum* group.

Dictyonema subtile (Přídolí and Devonian) and *D*. sp. cf. *D. subtile* (Ludlow) may represent gracile offshoots from the main lineage, although *D. subtile* maintains the low dissepimental

spacing (1-3 per cm), whereas *D*. sp. cf. *D. subtile* is unusual in having 15 dissepiments per cm. These graptolites are exceedingly slender, and far less likely to survive high energy depositional environments than more robust species.

OTHER DENDROID GRAPTOLITE GENERA

Although almost 50% of recorded benthic Silurian dendroids in the strata investigated belong to *Dictyonema* we have also recorded 10 other genera referable to at least 30 species (see Fig. 3 for stratigraphic ranges). However, the record is not good enough for us to make other than a few evolutionary comments. For example, it seems likely that *Acanthograptus aculeatus aculeatus* from the *nilssoni* to *praecornutus* levels of the Ludlow gave rise to *A. a. neureaensis* from the late Ludlow *inexpectatus*/*kozlowskii* biozones. This evolutionary change would have involved gracilisation of the rhabdosome and development of more diminutive autothecae. Most graptolite lineages produced gracile and, indeed, robust offshoots, from time to time, so there is nothing unusual in this particular change.

Similarly, *Acanthograptus deckeri* Bouček, 1957, from the early Ludlow of Bohemia, is probably preceded in an evolutionary sense by *A. praedeckeri praedeckeri* (*turriculatus* to *griestoniensis* biozones) and its gracile offshoot *A. p. minimus* (*crispus* Biozone). This particular lineage of *Acanthograptus* is probably quite separate from the *A. aculeatus* lineage suggested above, the latter being much more slender with more twigs and a less bushy rhabdosome (see Rickards *et al*. 2003, p. 324).

Callograptus J. Hall, 1865 is represented in Australia by six forms, but any relationship between them is not clear, each form having quite striking stipe arrangements. As pointed out by Rickards *et al*. (2003, p. 310) the distinction between *Dictyonema* and *Callograptus* rests almost wholly on the almost total absence of dissepiments in the latter and may be to some extent rather artificial. However, we cannot link any of the described callograptids with the dictyonemid lineages described here. It is possible that callograptids have relatively simple autothecae – although more work is needed on better material – and in this case only the *venustum* lineage among the dictyonemids is likely to have been similar. And, of course, most species in the *venustum* lineage have very low dissepimental spacings. We propose no evolutionary lineages for *Callograptus* or links with the described *Dictyonema* lineages.

Dendrograptus J. Hall, 1858, widely considered the evolutionary root of all dendroid graptolites, is quite rare in Australian strata and only occasionally well enough preserved to warrant detailed description, exceptions being the *Dendrograptus* spp. from Four Mile Creek (Rickards *et al*. 2003; Fig. 3 herein). Fragments of unidentifiable broken *Dendrograptus* occur occasionally in the Silurian and the Devonian, and it may be that the optimum environment for the genus was close inshore.

Stelechocladia Počta, 1894 is a *Dendrograptus*-like genus quite well represented in Australia in comparison with other regions except for Bohemia. Like *Callograptus*, it survived relatively intact without the support of dissepiments, and may have been adapted to a quieter water environment than *Dendrograptus*. We cannot distinguish any evolutionary lineages in *Stelechocladia*.

Thallograptus Ruedemann, 1925, is represented in Australia by five species, and fragments of the genus are common. Much better sequences of thallograptids will be needed before evolutionary relationships can be clarified; this situation is exacerbated by the lack of thecal details in most described species.

The following dendroid genera occur in Australia, but no comments are made as information beyond a few described species is lacking: *Palaeodictyota* Whitfield, 1902; *Ptilograptus* J. Hall, 1865; *Pseudodictyonema* Bouček, 1957; *Koremagraptus* Bulman, 1927; and *Desmograptus* Hopkinson in Hopkinson & Lapworth, 1875.

In addition to the dendroid graptolites we have listed in Figure 3, other hemichordates (excepting graptoloids) occuring in Australian Silurian strata are the tuboids *Galeograptus* Wiman, 1901; *Reticulograptus* Wiman, 1901; *Cyclograptus* Spencer, 1884; and the rhabdopleuran hemichordate ?*Rhabdopleura* sp. (see Rickards *et al*. 2009). All are known only from scattered occurrences, like the dendroids of the preceding paragraph.

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